REPRODUCTIVE BIOLOGY OF STELLER SEA LIONS IN THE GULF OF ALASKA

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ABSTRACT.—Reproductive biology of Steller sea lions (*Eumetopias jubatus*) in the Gulf of Alaska was studied between 1975 and 1979 by examination of reproductive tracts, estimation of ages from dental annuli, and observations at rookeries and hauling areas. Timing of key reproductive events was: 1) birth, mid-May to mid-July; 2) breeding, late-May to mid- or late-July; and 3) implantation, late-September and October. The female-pup bond usually was 1 year, however, 1-, 2-, and 3-year-old animals occasionally were seen to suckle females. Some males became sexually mature by 3 years and all were sexually mature by 8 years. Mature males had seasonal spermatogenic activity with abundant epididymal spermatozoa from late April through July. Initial ovulations and pregnancies occurred between 2 and 8 years of age. The average age at first ovulation was 4.6 ± 0.8 years (95% confidence limits) and first pregnancy 4.9 ± 1.2 years. Ovulation rates ranged from 26% at 3 years to 100% for animals ≥6 years. Incidence of pregnancy ranged from 20% at 3 years to 87% for females 8 to 20 years. Prenatal mortality between implantation and birth was estimated at 4.7% per month. The annual birth rate of full-term pups was estimated to be about 63% for sexually mature females.

This is a report on a study of the reproductive cycle, age at sexual maturation, and reproductive rates of Steller sea lions (*Eumetopias jubatus*). The investigation was conducted in the Gulf of Alaska between Cape St. Elias and Sanak Island (Fig. 1); an area containing an estimated 110,000 to 140,000 Steller sea lions, 10 major breeding rookeries, and a minimum of 50 hauling areas.

Most published information on reproduction in Steller sea lions was limited to observations of animals at rookeries and hauling areas (Pike and Maxwell, 1958; Mathisen et al., 1962; Thorsteinson and Lensink, 1962; Orr and Poulter, 1967; Edie, 1977). These investigators documented social and behavioral aspects of reproduction and provided information on timing and sequence of reproductive events. Some estimates of birth rates were made from counts of females and pups. Steller sea lions are described as gregarious, polygynous animals that gather annually at traditional rookeries where pupping and breeding take place. The larger, fittest males defend territories within rookeries where females give birth to a single pup and breed. We are aware of only two limited studies based on collected specimens to assess reproduction in Steller sea lions. Perlov (1971) found that females first ovulated at 3 to 5 years and that males matured between 5 and 7 years based on 115 sea lions collected in the Kurile Islands. Ages of 160 territorial bulls collected in the Gulf of Alaska by Thorsteinson and Lensink (1962) ranged from 5 through 15 years. They also suggested that biennial breeding of females occurred.

There was an obvious paucity of information on portions of the reproductive cycle of Steller sea lions and inadequate estimates of reproductive rates and age at sexual maturation. Therefore, the objectives of our study were to determine (1) the chronology of the reproductive cycle, (2) whether or not delayed implantation occurred, (3) the type and extent of reproductive failures, (4) reproductive rates, and (5) age at sexual maturation.

METHODS

Between February 1975 and September 1978, 138 female and 97 male sea lions were collected by shooting on rookeries, hauling areas, and in coastal waters. Ovaries, uteri, and epididymides were preserved in 10% formalin. Each uterus was opened and examined for the presence of an

embryo or fetus and placental attachment sites. Ovaries were sectioned at about 1 mm with a scalpel and examined for follicles, corpora lutea, and corpora albicantia. When possible, females were classified according to reproductive status—nulliparous, primiparous, or multiparous—and to reproductive conditon: not pregnant, ovulated, implanted pregnant, embryo being resorbed, or fetus aborted. Epididymal smears were examined under the microscope to determine the presence and relative abundance of spermatozoa.

Second upper premolars from specimens were decalcified, sectioned at about 48 micra, and stained with hematoxylin. Ages were estimated from counts of cementum annuli. Annual deposition of cementum annuli was confirmed by examination of sectioned teeth from nine known-aged animals (branded as pups). Both Fiscus (1961) and Spalding (1964) used dental annuli to estimate ages of Steller sea lions.

Nearly daily observations of sea lions on portions of two large pupping rookeries on Sugarloaf Island (13 April–15 July 1978) and Marmot Island (7 May–9 July 1979) and at the Cape St. Elias hauling area (9 March–14 June 1977; 22 March–5 July 1978) were made to ascertain timing and duration of birth and breeding seasons, incidence of abortions, lactation, and weaning. Sightings of known-aged females nursing pups and known-aged animals suckling females provided information on sexual maturation, weaning, and duration of mother-offspring bonds.

Results and Discussion

We observed births of surviving pups between 13 May and 14 July. Nearly 70% of 6,000 births (based on cumulative counts of pups) recorded on Sugarloaf Island in 1978 and Marmot Island in 1979 occurred between 5 and 16 June.

Timing and duration of pupping on rookeries from California to the Bering Sea appeared to be similar, mid-May to mid-July, with a peak in June (Scheffer, 1945; Pike and Maxwell, 1958; Thorsteinson and Lensink, 1962; Gentry, 1970; Mate, 1973; Edie, 1977).

Female-offspring bonds appeared to last less than 1 year in most instances as about 63% of mature females gave birth to full-term pups annually and females accompanied by young of more than one age class were not observed commonly. However, we sometimes saw subadults (1–3 years), including known-aged animals to 37 months of age, suckling females. Milk was found in the stomach of a 39-month-old female.

Some weaning appeared to occur late in the gestation period as significantly fewer ($\chi^2 = 4.27$, $P < 0.05$) multiparous females were lactating between 12 April and 28 May (17 of 28, 61%) than between 24 June and 22 March (41 of 50, 82%). There was no discernible correlation between lactation and pregnancy status as the proportions of mature, nonpregnant females (13 of 16, 81%) and mature, pregnant females (43 of 60, 72%) that were lactating were not significantly different ($\chi^2 = 0.60$, $P > 0.30$).

Rare (<1% of observations of nursing females) instances of females nursing two individuals simultaneously were seen and included females nursing subadults, one subadult and one pup, and two pups. One large female nursed a smaller female that, in turn, was nursing a subadult. Milk was seen to flow from nipples of both females. Pups were seen to surreptitiously suckle a female that was nursing another pup and quickly lie down when the female looked back, indicating that animals sometimes suckled females other than their mothers. One recognizable female was seen to nurse two different subadults repeatedly during a 17-day period.

Sandegren (1970) listed four ways in which mother-offspring bonds could last more than a single year: 1) females did not give birth every year and retained the bond with their young into the second year; 2) females renewed the bond with their last young after loss of a pup; 3) females rejected the newborn and kept the older offspring; and 4) the female kept both pup and yearling. He observed suckling subadults of at least two age classes including some nearly as large as their mothers.

Different proportions of mature females accompanied by nursing subadults were reported; 2% in California (Gentry, 1970), 12% in Oregon (Mate, 1973), 25% in British Columbia (Pike and Maxwell, 1958), 31.6% in British Columbia (Edie, 1977), 81% in

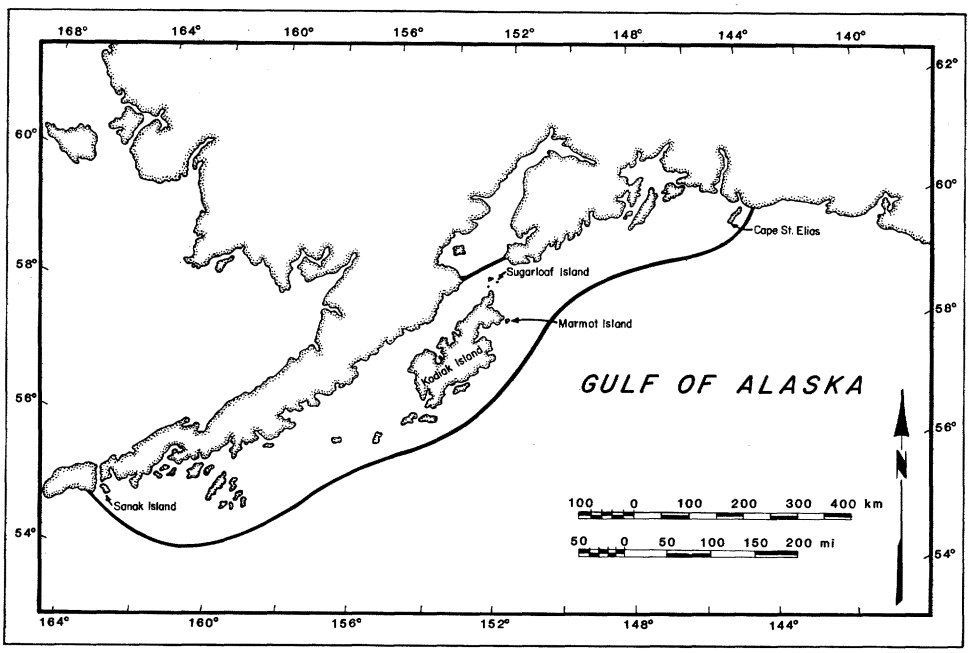

FIG. 1.—Study area of Steller sea lions in the Gulf of Alaska.

Alaska (Sandegren, pers. comm., as cited by Mate, 1973). On Marmot Island we found 28% of adult females accompanied by subadults, whereas on Sugarloaf <1% of the females were with subadults. Mate (1973) suggested a north-south clinal gradation in length of the nursing period. However, it seems to us that the observed differences in proportions of nursing subadults probably were related to the type of areas where the observations were made—rookeries, hauling areas, or combinations of these. The two extremes were both in Alaska. Sandegren's (pers. comm., as cited by Mate, 1973) estimate of 81% was from a hauling area where few pups were born. The <1% estimate was from Sugarloaf, which was primarily a rookery.

Copulations were observed between 22 May and 12 July; however, limited breeding must have occurred after this date as a few pups were still being born when intensive observations terminated on 15 July. Most (98%) of 215 copulations seen on Marmot Island in 1979 were between 7 June and 4 July.

Both Gentry (1970) and Sandegren (1970) were able to recognize individual females and to calculate the time elapsed between birth and copulation. Gentry reported that females bred from 6 to 16 days after giving birth ($\bar{X}$ = 11.4 days), whereas Sandegren (1970) found that breeding occurred from 10 to 14 days after giving birth ($\bar{X}$ = 11.8 days).

Data on male reproduction were limited by the small number (18) collected during the breeding season. Males were considered mature if abundant epididymal spermatozoa were found during the breeding season (Hewer, 1964; Bigg, 1969). Proportions of mature males by age class were as follows: 0 to 2 years, 0 of 5; 3 years, 1 of 4; 4 years, 0 of 1; 5 years, 1 of 1; 6 years, 0 of 1; 8 to 18 years, 6 of 6. These data generally support the findings of Perlov (1971) that males mature between 5 and 7 years of age. Thorsteinson and Lensink (1962) found that ages of 160 territorial bulls ranged from 6 to 15 years with most (88%) between 9 and 13 years. Therefore, it seems that most males mature sexually before they are able to defend breeding territories.

TABLE 1.—*Ovulation and pregnancy rates for female Steller sea lions collected in the Gulf of Alaska, February 1975 to September 1978.*

Age (years)	Ovulation			Pregnancy		
	Number in sample	Number ovulated	Ovulation rate (%)	Number in sample	Number pregnant	Pregnancy rate (%)
0–1	6	0	0	6	0	0
1	7	0	0	6	0	0
2	11	0	0	10	0	0
3	19	5	26.3	15	3	20.0
4	16	13	81.3	15	8	53.3
5	10	8	80.0	7	4	57.1
6	7	7	100.0	6	5	83.3
7	12	12	100.0	10	7	70.0
8	9	9	100.0	6	6	100.0
9	6	6	100.0	6	5	83.3
10	6	6	100.0	6	5	83.3
11–15	22	22	100.0	23	20	87.0
16–20	4	4	100.0	5	4	80.0
21–30	3	3	100.0	3	0	0
Totals	138	95		124	67	

Seasonal spermatogenic activity in mature males (≥7 years) was apparent as all nine mature males collected between 20 April and 1 August had abundant epididymal spermatozoa. Conversely, none of eight mature males collected between 27 October and 22 March had abundant spermatozoa.

Although most female Steller sea lions bred between late May and mid-July, the blastocyst apparently did not implant until late September or October. Eight mature females collected between 24 June and 1 August had ovulated and a corpus luteum was present in an ovary from each animal. No embryos or implantation sites were found in the uteri. Ten of 11 mature females collected between 7 and 14 October had small, implanted embryos that weighted between 0.01 and 25.9 g. The other female had a corpus luteum, but no embryo or implantation site was found. She may have been in the delay of implantation or failed to become pregnant. All seven mature females collected between 27 October and 15 November had implanted embryos.

A small (0.4 g) embryo was found in the uterus of a female collected on 11 February. The embryo was comparable in size to those collected in October just after implantation. The average weight of 17 fetuses from females collected from 11 to 16 February was 4,255 g.

We are not aware of previously published reports of delayed implantation in Steller sea lions, although J. S. Vania (pers. comm.) postulated a 3-month delay based on the examination of reproductive tracts from 11 females.

First ovulations in our sample of female sea lions occurred between 3 and 8 years of age with the following distribution: 0 to 2 years, 0; 3 years, 5; 4 years, 6; 5 years, 2; 6 years, 3; 7 years, 1; 8 years, 1; 9 to 30 years, 0. The average age at first ovulation was 4.6 ± 0.8 years (95% confidence interval). Initial pregnancies also occurred between the ages of 3 and 8 years: 0 to 2 years, 0; 3 years, 3; 4 years, 2; 5 years, 2; 6 years, 2; 7 years, 1; 8 years, 1; 9 to 30 years, 0. The average age at first pregnancy was 4.9 ± 1.2 years (95% confidence interval). Numbers of reproductive tracts examined for each age class are included in Table 1.

Observations were made of a known-aged, 3-year-old female that nursed a pup on Marmot Island during the summer of 1979. This indicated ovulation and breeding at 2 years of age and parturition at age 3, apparently a rare occurrence because examination of reproductive tracts from 11 2-year olds and 19 3-year olds showed no evidence of ovulation in 2-year-old animals.

TABLE 2.—*Summary of reproductive failures in Stellar sea lions collected in the Gulf of Alaska, February 1975 to September 1978.*

Age (years)	Initial pregnancy	Cause of failure			
		Preimplantation failure	Resorption	Abortion	Indeterminable
3	Yes	X			
4	Unknown	X			
4	Yes		X		
4	Yes				X
4	Yes	X			
5	No			X	
6	No			X	
7	No			X	
7	Yes			X	
7	No				X
7	No				X
8	No			X	
9	No		X		
10	No			X	
11	No			X	
13	No			X	
19	No				X
21	No				X
25	No				X
30	No				X

Perlov (1971) concluded that females from the Kurile Islands first ovulated at 3 or 4 years of age. All 5-year olds had ovulated and by 7 years all had borne pups. These results were nearly identical to ours except we found a wider range of maturation ages as might be expected in a larger sample.

Annual rates of ovulation increased from 26% at 3 years of age to 100% by 6 years (Table 1). All females 6 years old and older that we examined had ovulated in the year they were collected. Observed pregnancy rates increased from 20% at 3 years to 87% for females between 8 and 20 years (Table 1). None of three females older than 20 years was pregnant, possibly indicating reduced fecundity in older age classes. Pregnancy rates of northern fur seals (*Callorhinus ursinus*) declined slowly with age after 10 years (Chapman, 1964); however, reproductive senility was not detected in several species of Phocidae (Smith, 1973).

Reproductive failures were classified according to the following terminology: 1) preimplantation failure in which females ovulated and either fertilization did not occur or the blastocyst failed to implant; 2) resorption of an embryo; and 3) abortion. Evidence of reproductive failure was found in 20 of 85 sexually mature females collected throughout implanted gestation (Table 2). Preimplantation failures occurred in younger animals and appeared to be associated with initial ovulations, a relationship similar to that in northern fur seals (Craig, 1964). Resorptions were found twice, once in a young female during an initial pregnancy and once in a multiparous female. Abortions occurred throughout a wide range of ages in mostly multiparous females. We frequently saw evidence (69 cases) of abortions on haulout areas. Forty-one abortions were documented at Cape St. Elias, 22 of which occurred in March.

Gentry (1970) reported that abortions of Steller sea lions on Año Nuevo Island, California, began in February and continued until mid-May when surviving pups appeared. In Oregon, abortions were estimated to account for 4% of total births (Mate, 1973). Abortions in California sea lions (*Zalophus californianus*) were associated with disease (Smith et al., 1974; Smith and Akers, 1976), organochlorine pollutants (Delong et al., 1973), and element imbalance (Martin et al., 1976).

The birth rate (full-term pups) was lower than pregnancy rates (Table 1). Pregnancy rates were calculated from females collected throughout the period of implanted gestation. Reproductive failures occurred throughout gestation; therefore, pregnancy rates progressively declined: Oct.–Nov., 95% (n = 19); Feb.–March, 76% (n = 34); April–May, 67% (n = 36). Abortions continued throughout mid-May; therefore, the birth rate was slightly lower than the 67% pregnancy rate for April and May. The declining pregnancy rates indicated a monthly prenatal mortality rate (assuming a linear relationship) of 4.7%, resulting in a projected birth rate of about 63% for sexually mature females.

Gentry (1970) estimated the birth rate for Steller sea lions on Año Nuevo Island at 68% based on counts of pups and females. He believed the estimate might be high because some females possibly were at sea while their pups were on land when counts were made. By use of the same method, Pike and Maxwell (1958) estimated a birth rate in excess of 70% for sexually mature females on a rookery in British Columbia.

Thorsteinson and Lensink (1962) suggested that biennal breeding is characteristic of Steller sea lions. Our findings of annual ovulation rates of 100% for females 6 years old and older, pregnancy rates of 95% during early-implanted gestation, and annual birth rates of about 63% indicated that annual breeding occurred at least during the period when our study was conducted.

Our estimates of reproductive rates and age at sexual maturation provide a basis from which analyses of population dynamics can be made when additional data on population composition and survivorship are obtained. These estimates also form a base for comparisons with other populations or the same population in the future. Comparisons of these parameters may be valuable in evaluating relative status of a population (DeMaster, 1978; Eberhardt, 1977; Eberhardt and Siniff, 1977).

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